

SEXUAL DIMORPHISM IN THE BELEMNITE *YOUNGIBELUS* FROM THE LOWER JURASSIC OF YORKSHIRE

by PETER DOYLE

ABSTRACT. Two belemnite species, *Youngibelus tubularis* (Young and Bird) and *Y. levis* (Simpson), are described from one 7.6 m bituminous shale horizon in the *falciferum* Subzone of the Yorkshire Toarcian. Ontogenetic studies show a common identity for the two species in their initial growth stages (nepionic, neanic). Divergence in morphology occurs in late growth (gerontic stage) by the development of an epirostrum in *Y. tubularis* and rostral thickening in *Y. levis*. It is concluded that *Y. tubularis* and *Y. levis* are dimorphs of a single biological species. Further, it is postulated that the epirostrum was used for counterbalancing a sexual adaptation or for courtship display purposes. Both forms are described as separate morphospecies.

DETAILED bed-by-bed collecting in the *falciferum* Subzone of the Yorkshire Toarcian has suggested a dimorphic relationship between the two belemnite species *Y. tubularis* (Young and Bird 1822) and *Y. levis* (Simpson 1855). Previously, these species have been included in different genera (e.g. Lissajous 1925; Sachs and Nal'njaeva 1975). They occur in one 7.6 m bituminous shale horizon in the mid *falciferum* Subzone. This is well exposed on the foreshore at Saltwick Bay (bed 43 of Howarth 1962). South-east of the Peak fault it is represented by the top of bed x, the Peak stones (bed xi), and the base of bed xii, which are well exposed on the foreshore between Blea Wyke Point and Peak Steel, Ravenscar.

The restriction of *Belemnites tubularis* to one horizon was recognized by most of the early workers including Simpson (1866, 1884), Phillips (1867) and Tate and Blake (1876). Notes found with the Phillips collection in the Oxford University Museum refer to a 'tubularis bed' and the association of *Y. levis* with *Y. tubularis* was evidently known to Phillips, as specimens of *Y. levis* in the Museum are labelled: 'With *B. tubularis*, Saltwick.' Both species are usually very well preserved in this bituminous shale. It is common to find the phragmocone in place with generally the first twenty or so camerae undamaged. Pyrite commonly replaces septal walls and infills the camerae. Fine rostral detail is usually visible.

A total of eighty-three specimens of *Y. levis* and sixty-one of *Y. tubularis* have been collected by the author and Dr. P. F. Rawson, most of which are currently housed in the Department of Geology, University College London. A further forty-six specimens of *Y. levis* and thirty-five specimens of *Y. tubularis* have been examined in the collections of the British Museum (Natural History), the Oxford University Museum, and the Whitby Museum.

At present there is no comprehensive text which outlines detailed belemnite skeletal morphology. Therefore, a short glossary of the more unfamiliar terms is given below. Further details may be found in Roger (1952) and Stevens (1965).

Apical line. Axis of rostrum marked by successive positions of the apex during growth.

Compressed. Rostrum with greater dorsoventral than lateral diameter.

Conorostrid. Conical form of juvenile (nepionic) rostrum (also *Clavirostrid*, club form juvenile rostrum).

Depressed. Rostrum with greater lateral than dorsoventral diameter.

Endogastric. Ventral incurvature of the protoconch.

Epirostrum. Tube-like posterior prolongation of normal rostrum (*orthorostrum*), consisting of a central mass (*corpus pulposum*) surrounded by walls exhibiting typical belemnite structure.

Lateral lines. Weak linear markings on the rostral flanks possibly indicating point of fin attachment.

Ortholineate. Straight, centrally situated apical line undeflected ventrally (also *cyrtolineate*, strongly ventrally curved apical line; *goniolineate*, straight apical line close and almost parallel to venter).

Orthorostrum. True or first-formed rostrum of epirostrate belemnites, exhibiting typical concentrically layered and radially prismatic structure.

Outline. Ventral or dorsal aspect of rostrum.

Primordial rostrum. Larval (usually dish-like) rostrum attached to the distal end of protoconch.

Profile. Lateral aspect of rostrum.

The following abbreviations are used: BM, British Museum (Natural History); OUM, Oxford University Museum; WM, Whitby Museum; L, length from protoconch to apex of rostrum; D, dorsoventral diameter at the protoconch; DI, lateral diameter at the protoconch.

SYSTEMATIC DESCRIPTIONS

Subclass COLEOIDEA Bather, 1888

Order BELEMNITIDA Zittel, 1895

Suborder BELEMNITINA Zittel, 1895

Family BELEMNITIDAE d'Orbigny, 1845

The above classification is that recognized by Jeletzky (1966) who considered the nomenclaturally invalid Polyteuthidae Stolley, 1919 to be a junior synonym of the Belemnitidae d'Orbigny. Riegraf (1980) recognized the Polyteuthidae, including within it the Belemnitidae as used by Jeletzky, plus the Cylindroteuthididae Stolley, 1919.

Subfamily MEGATEUTHINAE Sachs and Nalnjaeva, 1967

Genus YOUNGIBELUS Riegraf, 1980

Type species. *B. tubularis* Young and Bird, 1822.

Emended diagnosis. Very slender, moderately long to long, cylindrical to cylindriconeal rostra with moderate to strong lateral compression. Transverse sections elongate subquadrate to pyriform. Apical grooves absent or residual, but apical striae commonly well developed. Epirostrum may be developed extending the total length of the rostrum to three times that of orthorostrum. Lateral lines consist of two shallow depressions separated by a weak 'weal' along the length of the orthorostrum. Apical line ortholineate, phragmocone central with slight endogastric (ventral) incurvature of the protoconch. Alveolar angle 27°.

Stratigraphic range. Upper part of the lower Toarcian of Britain, Germany, France, and ?Siberia.

Discussion. *Youngibelus* differs from *Acrocoelites* by its lack of strong apical grooves, from *Dactyloteuthis* by its long slender cylindriconeal shape and ortholineate apical line, and from *Salpingoteuthis* by its well-developed orthorostrum and lack of strong 'canals' on its flanks.

Species included are *Y. tubularis* (Young and Bird), *Y. gigas* (Quenstedt), and *Y. levis* (Simpson). *B. tripartitus gracilis* Quenstedt, assigned to *Youngibelus* by Riegraf (1980), is excluded due to its strong apical grooves. It is probably a species of *Acrocoelites*.

EXPLANATION OF PLATE 14

Figs. 1-5. *Youngibelus tubularis* (Young and Bird), ×1. 1-4, right lateral and ventral views. 1, BM C59185, neotype, epirostrum uncrushed, Saltwick. 2, BM C59186, rostrum with anterior wrinkling, epirostrum crushed, Saltwick. 3, BM C59200, rostrum with crushed epirostrum, Ravenscar. 4, BM C59199, orthorostrum with apical scar of missing epirostrum, Ravenscar. 5, BM C59192, longitudinal section (venter to right), epirostrum uncrushed, Ravenscar.



DOYLE, *Youngibelus*

Youngibelus tubularis (Young and Bird 1822)

Plate 14, figs. 1-5

- * 1822 *Belemnites tubularis* Young and Bird, p. 259, pl. xiv, fig. 6.
- 1829 *Belemnites tubularis* Young and Bird; Phillips, p. 163, pl. xii, fig. 20.
- v1855 *Belemnites tubularis* Young and Bird; Simpson, p. 23.
- v1855 *Belemnites productus* Simpson, p. 216.
- vp1867 *Belemnites tubularis* Young and Bird; Phillips, p. 68, pl. xiv, fig. 36 (*non*. p''-p''').
- 1920 *Cuspitoothis tubularis* (Young and Bird); Bülow-Trummer, p. 107.
- 1925 *Dactylotheuthis tubularis* (Young and Bird); Lissajous, p. 148.
- 1969 *Belemnites tubularis* Young and Bird; Schwegler, p. 206, text-fig. 87.
- 1980 *Youngibelus tubularis* (Young and Bird); Riegraf, p. 149.

Diagnosis. Long *Youngibelus* with epistrostrum. Outline and profile symmetrical. Transverse sections of orthostrum pyriform to elliptical, of epistrostrum almost circular. Surface of rostrum commonly wrinkled in the alveolar region.

Type specimens. Young's collection was deposited in the Whitby Museum. However, there is no evidence that any of the *B. tubularis* in the Museum were once in the possession of Young. They all bear Martin Simpson's labels and probably were collected by him. One specimen, No. 678, is similar in some respects to Young and Bird's pl. xiv, fig. 6, but it has been remounted on a block of shale with large numbers of crushed Dactylioceratids. This also was apparently collected from High Whitby and not Saltwick. With no proven syntypes remaining from which to select a lectotype, a neotype is here designated.

Young and Bird's *stratum typicum* is the 'Alum Shale' of Saltwick: 'Alum Shale' embraced the whole of the Upper Lias. The beds exposed in Saltwick Bay are of *falciferum* Subzone, with bed 43 (Howarth 1962) exposed on a large proportion of the shore. As *B. tubularis* is common within this horizon it can be assumed that Young obtained his syntypes here. Hence specimen BM C59185 (Doyle Collection) (Pl. 14, figs. 1, 2) from bed 43 of Saltwick is designated neotype.

Locality and material. Saltwick Bay and Ravenscar, *falciferum* Subzone (bed 43 and its equivalents of Howarth 1962). BM thirty-four specimens: Blake Collection (C11985-11987), Wright Collection (C42212-42215), and C9681-9685, C2288 (ten specimens), C3655, 15996, 15997, 37596, C57355, C405 (two specimens), 83687, 88949. OUM, seven specimens: Phillips Collection (J38036, J38037, J15101, J15108, J15109) and J38274, J37676. WM, six specimens: old no. 59, no. 678, and four unregistered.

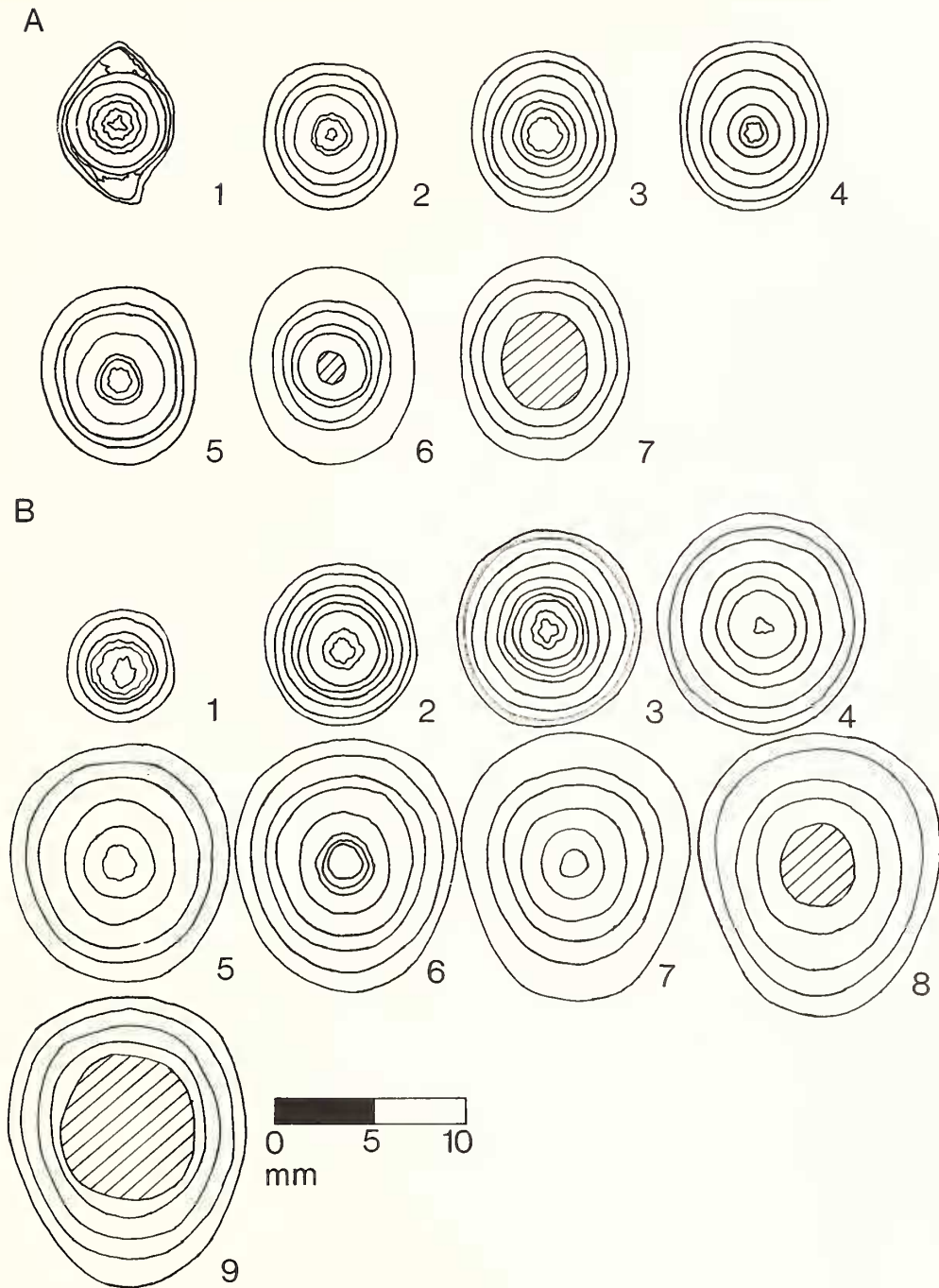
Description. Rostrum very elongate and slender, length of the orthostrum about six times that of the transverse diameter at the protoconch. Dimensions of figured section: L, 61.5 mm; D, 9.6 mm; D1, 7.5 mm. The outline is symmetrical and subcylindrical, with a slight adoral flaring. The apex of the orthostrum is mucronate and slightly attenuate protruding into the epistrostral fabric. The apex of the epistrostrum is generally compressed, but where it is preserved it is acute, with very gentle divergence. The profile is less symmetrical than the outline, with a slightly more inflated venter. A constriction tends to develop where the epistrostral wall meets the orthostrum. This gives the impression of flaring from the almost cylindrical epistrostrum.

Transverse sections reveal that the orthostrum is generally compressed for most of its length, the epistrostrum less so. There is no marked depression of the rostrum. The sections of the orthostrum are pyriform in shape. No apical grooves are present, but apical striae are commonly well developed. Those on the apex of the orthostrum may be more incised than those on the apex of the epistrostrum.

Wrinkles of the surface of the rostrum at the alveolar end are a common trait of this species; more extreme examples were separated by Simpson (1866) as *B. productus*. Lateral lines take the form of long shallow areas in a ventrolateral position. These are separated by a 'weal', common to most members of the Megateuthinae.

The phragmocone occupies a central position with the protoconch slightly incurved ventrally. The phragmocone penetrates approximately one-third of the orthostrum. The apical line is ortholineate, the alveolar angle 27°.

Structure of the ortho- and epistrostrum. The orthostrum consists of concentric growth layers of laminae pellucidae (light unobscured calcite). The walls of the epistrostrum consist of the same material. These thin (0.5 mm) epistrostral walls form a tube which is filled with an apparently structureless porous mass (*corpus pulposum* of Muller-Stoll 1936). Where they join the orthostrum, the epistrostral walls become its last concentric growth lamellae. The apical third of the orthostrum protrudes into the epistrostral 'cavity'. This 'cavity' is



TEXT-FIG. 1. Transverse sections of *Youngibelus tubularis* and *Y. levis* from Saltwick Bay. Sections at 5 mm intervals (section numbers indicating approximate length). Alveolus hatched. Venter lowermost. A, *Y. tubularis*, BM C59190, sections 1-8 of orthorostrum. The epirostrum is crushed in the lateral plane (section 1). B, *Y. levis*, BM C59198, sections 1-11 of rostrum.

infilled with a highly porous and granulose mass, which seems to have crude growth lines mimicking the apex of the orthorostrum. No trace of the radiating, recrystallized prisms of the orthorostrum are seen here, although holes in the epirostral mass indicate diagenetic alteration (Spaeth, Hoefs and Vetter 1971).

Ontogeny

Transverse sections. The terms nepionic, neanic, and ephebic-gerontic introduced by Fischer (1947) and discussed by Pugaczewska (1961) are used to describe the ontogeny. The section of the nepionic stage is pyriform with the venter broadest. This stage, like all subsequent stages, has strong striae at its apex, giving a corrugated aspect to the growth lines (text-figs. 1A, 2A). The neanic growth stage marks a departure from a pyriform to a more elliptical section. In the alveolar region the section is characterized by a more quadrate shape, changing to an elongate ellipse in the stem region. The change from the nepionic pyriform to neanic elliptical section is gradual. The apex is striated (text-fig. 1A, 2A). The ephebic-gerontic stage shows a reversion to a pyriform section, although less pronounced than in the nepionic stage. However, in this stage the dorsum is broadest, a complete reversion from the nepionic stage (text-figs. 1A, 2A). The gerontic stage includes the development of the epirostrum, epirostral walls becoming the final growth layers. Sections of the epirostrum have an almost circular shape.

Longitudinal sections. The nepionic growth stage of *Y. tubularis* has a conorostrid (conical) form. The neanic stage is represented by a more elongate form of the nepionic rostrum. The ephebic-gerontic growth stage is characterized by a rapid elongation of the rostrum, culminating in the development of an epirostrum. The last growth layers of the orthorostrum display this elongation with respect to the width. Development of the epirostrum was obviously a late-stage feature (see also Krimholz 1958), the epirostral walls growing out from the orthorostrum, followed by the infilling of the epirostral cavity. Text-fig. 3 shows the dramatic change from allometric to very strongly allometric growth in the ephebic-gerontic stage.

Discussion. Zieten's (1831) *B. longissimus* Miller closely resembles uncrushed specimens of *Y. tubularis*. Quenstedt's (1848) *B. acuarius tubularis* also appears to belong to *Y. tubularis*; the long ventral groove evident in the figure may well be pathological. The specimen figured by Phillips (1867, pl. xiv, fig. 36 p''-p''') is probably *Y. gigas* (Quenstedt). Werner's (1912) synonymy of *B. tubularis* included forms with pronounced apical grooves such as *B. tripartitus gracilis* Quenstedt and therefore his definition of the species only partly applies to the present one.

Youngibelus levis (Simpson, 1855)

Plate 15, figs. 1-6

- non 1836 *Belemnites laevis* Roemer, p. 165.
- v *1855 *Belemnites levis* Simpson, p. 25.
- v 1867 *Belemnites laevis* Simpson; Phillips, p. 57, pl. x, figs. 21, 25.
- v 1883 *Belemnites simpsoni* Mayer-Eymar, p. 641.
- 1920 *Cuspitethis laevis* (Simpson); Bülow-Trummer, p. 103.
- 1925 *Acrocoelites laevis* (Simpson); Lissajous, p. 103.

Diagnosis. Medium-sized *Youngibelus* without epirostrum. Outline symmetrical, profile nearly symmetrical, venter slightly inflated. Transverse sections pyriform.

Type specimens. Three syntypes are in the Whitby Museum (453a, b, c). All three display crushed apices. Syntype 453c is poorly preserved with greater than average compression; 453b has abnormally enlarged apical depressions; 453a is reasonably well preserved and displays all the common features associated with this species—it is here designated lectotype. This is probably the specimen figured by Phillips (1867, pl. x, fig. 231'').

EXPLANATION OF PLATE 15

Figs. 1-6. *Youngibelus levis* (Simpson), × 1. 1, 2, 4, 5, right lateral and ventral views. 1, 2, BM C59198, 59196, rostra from Ravenscar. 3, BM C59195, longitudinal section (venter to left), apex uncrushed, Saltwick. 4, 5, BM C59197, 59188, rostra from Saltwick. 6, BM C59191, longitudinal section (venter to left), apex crushed, Ravenscar.



1



2



3



4



5



6

DOYLE, *Youngibelus*

The syntypes were all collected from the 'Jet Rock, Upper Lias, near Whitby' (Simpson 1855, p. 25). This was later refined by Simpson (1884) to 'Division 5b, Upper Lias' (equivalent to bed 43 of Howarth 1962) from Saltwick. These specimens were later incorrectly labelled as coming from the '*communis*' Zone, Saltwick; beds exposed at Saltwick are of the *falciferum* Zone and Subzone.

Locality and material. Saltwick Bay and Ravenscar, *falciferum* Subzone (bed 43 and its equivalents of Howarth 1962). BM, seventeen specimens: Bean Collection (one, unregistered), Blake Collection (C11940-11942, C11944-11946), Wright Collection (C42218-42222, C42238, C42241) and C57090-57092. OUM, twelve specimens: Phillips Collection (J15258, J15260-15264, J15275, J15287-15289). WM, seventeen specimens: Simpson Collection (old nos. 453a, b, c; new nos. 332, 334, 335, 336, 337, 345-350, 358a, b, c).

Description. Rostrum of moderate size and generally slender, length about four times that of the transverse diameter at the protoconch. Dimensions of figured section: L, 47 mm; D, 13.5 mm; D1, 11 mm. The outline is symmetrical and subcylindrical. The apex terminates rapidly (0.2 of total length), leaving the rest of the outline cylindrical. The profile is slightly less symmetrical than the outline, the venter generally more inflated than the dorsum. The profile is cylindrical but with a general resemblance to the outline.

The transverse sections are compressed throughout the length of the guard, the emphasis shifting from dorsolateral to ventrolateral compression adorally. The sections are pyriform, with a broad venter. Depression is not marked in this species but may be developed in some individuals to a small degree. No definite apical grooves are present but the presence of slight depressions gives the impression of dorsolateral grooves. The apex is usually characterized by fine striations surrounding it. Lateral lines take the form of long flat areas subdivided into two subdepressions separated by a 'weal'.

The phragmocone is central, with the protoconch slightly endogastrically incurved. The phragmocone penetrates a third of the way into the rostrum. The apical line is ortholineate and the apical angle 27°.

Ontogeny

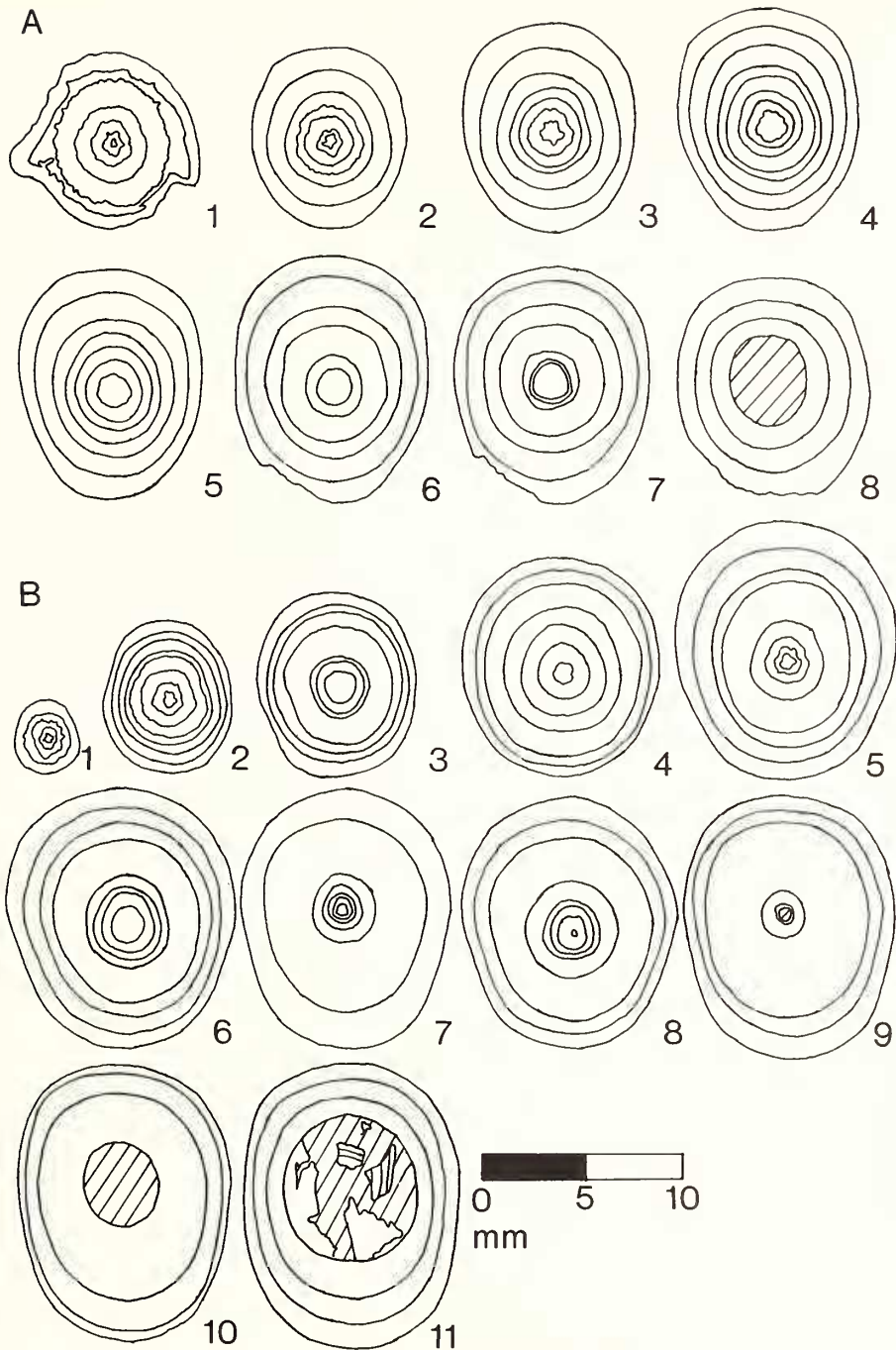
Transverse sections Three stages are recognized. The nepionic stage is characterised by a pyriform section with its maximum breadth at the venter. The apex is striated as in all subsequent stages (text-figs. 1B, 2B). The neanic stage shows a progression away from the pyriform section of the nepionic stage towards a more elliptical to subquadrate section (text-figs. 1B, 2B). This stage is also striated at the apex. In the ephebic-gerontic stage the surface morphology of the adult rostrum displays a section varying with its position relative to the rostrum. The apical region reveals a section which is pyriform resembling that of the nepionic stage. This is due to dorsolateral apical depressions. The stem region has a pyriform section with the dorsum broadest, a reversal from the neanic stage. This corresponds to an increasing ventrolateral compression adorally (text-figs. 1B, 2B.).

Longitudinal sections. The nepionic rostrum has a generally short conorostrid form. Growth proceeds in the neanic stage allometrically, but with relative increases of width to length. Gerontic growth is strongly allometric (text-fig. 3) with width increasing at a much greater rate than length. This results in a much stouter rostrum in the gerontic stage.

Discussion. This species closely resembles two described by Simpson (1855, 1884): *B. aptus* and *B. trivialis*. *B. aptus* may be an aberrant *Y. levis* with quite prominent apical grooves. *B. trivialis* has a similar shape and form, with apical striae and may be a juvenile *Y. levis* (as suggested by Phillips 1867 and Blake in Tate and Blake 1876).

B. levis Simpson was formerly considered to be a primary homonym of *B. laevis* Roemer. However, Simpson's original spelling omitted the 'a' attributed to this species by other authors. This one letter difference validates *B. levis* Simpson according to the International Code of Zoological Nomenclature. *B. simpsoni* Mayer-Eymar, erected to replace the homonym, therefore becomes a junior objective synonym of *B. levis* Simpson. *B. levis* was formerly placed in the genus *Acrocoelites* presumably due to its stratigraphical association with species of this genus and its differences from other Liassic genera. Lateral lines seen on *B. levis* are common in most members of the Megateuthinae. Sachs and Naljaeva (1975) transferred it to *Mesoteuthis*, presumably due to a lack of apical grooves. Bülow-Trummer (1920) came closest to identifying its true affinities when he placed the species in *Cuspoteuthis*.

B. levis is herein attributed to the genus *Youngibelus* for the following reasons: the species lacks apical grooves but has well-developed apical striae; it has a slender cylindrical shape with lateral compression and an ortholineate apical line; the central phragmocone is characteristic of the genus.

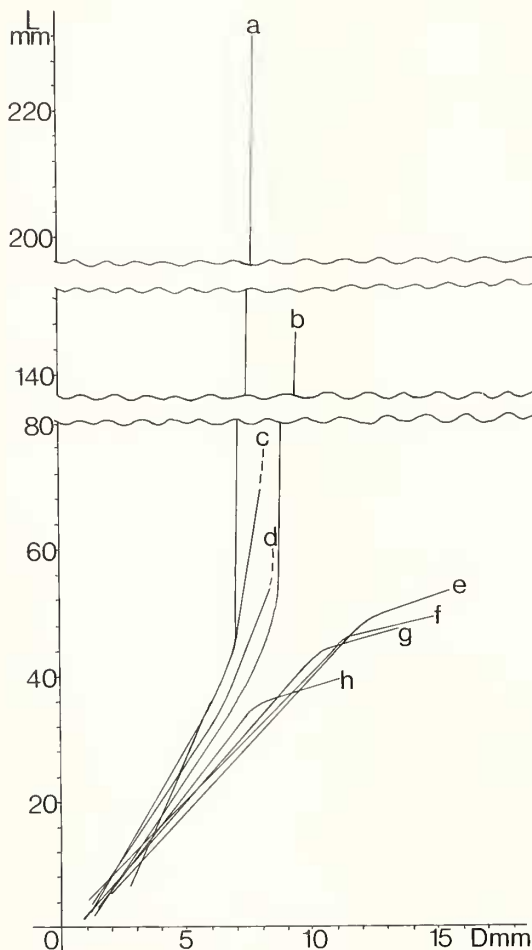


TEXT-FIG. 2. Transverse sections of *Youngibelus tubularis* and *Y. levis* from Ravenscar. Sections at 5 mm intervals (section numbers indicating approximate length). Alveolus hatched. Venter lowermost. A, *Y. tubularis*, BM C59194, sections 1-7 of orthorostrum. The epirostrum is crushed in the dorsoventral plane (section 1). B, *Y. levis*, BM C59193, sections 1-9 of rostrum.

THE ONTOGENY OF *Y. LEVIS* AND *Y. TUBULARIS*

The protoconch and primordial rostra take the same form in both species (text-fig. 3). The protoconch is nearly spherical, being slightly endogastrically incurved with respect to the rest of the pragocone. The primordial rostrum is in the form of a dish attached to the distal end of the protoconch. This type of primordial rostrum is commonly seen in members of the Belemnitina (Jeletzky 1966, p. 130).

The nepionic rostra of *Y. levis* and *Y. tubularis* are conorostrid, developing a more elongate version of this in the neanic stage which is also identical in both species. Postneanic development signals the change in form of both *Y. levis* and *Y. tubularis*. In the gerontic stage of *Y. tubularis* there is a relatively rapid increase in the length of the orthorostrum, with little change in the maximum diameter. The epirostrum is then developed, rapidly increasing the length of the whole rostrum by a factor of three. The epirostrum is an outgrowth of the final layers of the orthorostrum, the epirostral walls also covering the orthorostrum. This outgrowth was followed by the infilling of the epirostral cavity by the *corpus pulposum*. The gerontic stage of *Y. levis* is characterized, on the other hand, by the formation of a much stouter rostrum, the length increasing only slightly. This contrast between the two styles of gerontic development is well illustrated by the growth curves in text-fig. 3. Here



TEXT-FIG. 3. Growth curves of *Youngibelus tubularis* and *Y. levis*. *Y. tubularis*: a, BM C59214, b, BM C59192, d, BM C59217 (Ravenscar); c, BM C59218 (Saltwick). Specimens c and d have crushed epirostra, most of which are lost. *Y. levis*: f, BM C59195 (Ravenscar); e, BM C59191, g, BM C59216, h, BM C59215 (Saltwick).

the curves point to a practically identical early development with differentiation in the final growth stages. Differences between the early growth curves are due to specific variation, the variance within the *Y. tubularis* group being as great or greater than the differences between both species.

In transverse section the nepionic rostra of both species are pyriform with their maximum width at the venter. The neanic stage shows a more neutral elliptical section in both *Y. tubularis* and *Y. levis*. From here *Y. tubularis* develops a pyriform section with the dorsum widest. The increase in diameter of the rostrum is relatively small considering the great length attained in the gerontic stage. *Y. levis* has a similar pyriform section, but the increase in diameter is greater than that in *Y. tubularis*, corresponding to a relatively small increase in length.

It would seem, therefore, that before the gerontic stage the juveniles of both *Y. levis* and *Y. tubularis* are exactly alike in all aspects. After the neanic stage (the onset of sexual maturity) the two forms become separate. Throughout ontogeny the apical line remains central and the alveolar angle differs little between the two species.

SEXUAL DIMORPHISM

d'Orbigny (1842) was the first author to point to the possibility of differences between the sexes in belemnites. Subsequently the hypothesis has been touched upon by Phillips (1867), Lissajous (1925), Roger (1952), Waterston (1952), Delattre (1956), Stevens (1965), and Pinckney (1975). It is accepted that modern cephalopods show dimorphic characters to a greater or lesser degree (Westermann 1969) and the hypothesis of dimorphism in ammonites is also widely accepted (e.g. Makowski 1963; Callomon 1963; Palframan 1966). It therefore seems reasonable to expect dimorphism in belemnites.

Dimorphism in modern cephalopods takes the form of differences in size and this is also a common feature in ammonites. In belemnites, the function of the rostrum is seen primarily as a counterbalance for the main mass of the body tissue, head, and arms. If one sex were larger than the other, an increase in size of the rostrum to counterbalance the increased bulk of the body would be expected. The rostrum would be directly affected by sexual dimorphism manifested as a difference in size. d'Orbigny (1842), Waterston (1952), and Delattre (1956) claim to have recognized large and small forms of similar belemnites which they claim are dimorphic.

However, some workers (Stevens 1965; Pinckney 1975) believe that dimorphic characters would be more likely to occur beneath the pro-ostracum, where it is presumed the gonads were housed. They suggest that differences in length and form of belemnite rostra are more likely to be due to intraspecific variation. Riegraf (1981, p. 125) believed that it is difficult to recognize adult micro- and macro-rostra. He cited as an example *Y. tubularis*, for which no micro-rostrum could be found.

Makowski (1963) outlined four conditions which he considered prerequisites for the acceptance of dimorphism in ammonites:

1. Identical initial stages of ontogeny in both, with the identity of their phylogeny.
2. Lack of intermediate forms in the adult stages.
3. Presence of both forms in the same strata.
4. Numerical ratio of the two supposed sexes (sex ratio) comparable to that observed in living forms.

These criteria are also applicable to belemnites. As shown above, the ontogeny of *Y. tubularis* and *Y. levis* is identical in nepionic and neanic stages, differences only becoming apparent in the gerontic stage. Phylogenetically, both species have apparent parallel development, arising from the acrocoelid root stock (see Schwegler 1962). There are no intermediates between the adult growth stages of *Y. tubularis* and *Y. levis*. The presence of crushed apices in some examples of *Y. levis* cannot be accepted as true epistrostral development; it may be due to the resorption of growth layers as described by Muller-Stoll (1936) and Pugaczewska (1961). The stout *Y. levis* with slightly crushed apex cannot be described as intermediate between *Y. levis* with normal apex and the much more elongate and slender *Y. tubularis*.

Neither species has been found above or below bed 43 (*falciferum* Subzone) of Saltwick or its equivalents at Ravenscar. Both forms have been reported together from similar horizons in West Germany (Riegraf, pers. comm.). The sex ratios for the two associations at Ravenscar and Saltwick are 1·0:1·1 and 1·0:1·2 respectively. This is within acceptable limits for similar modern coleoid associations (Mangold-Wirz 1963).

FUNCTION OF THE EPIROSTRUM

The precise function of the epirostrum has remained a mystery for many years. Some authors (Muller-Stoll 1936; Roger 1952) suggested that it represents the last in a series of growth stadia occurring in all belemnites. Krimholz (1958) believed that its formation was almost accidental, due to a sudden elongation of the mantle, and that it cannot be tied down to any particular function. Recent authors (Jeletzky 1966; Seilacher and Wiesenauer 1978) believe that the epirostrum functions as a balancing aid, developed only in certain lineages where extra balance is required.

d'Orbigny (1842) suggested that the development of epirostra in *Dactyloteuthis acuarius* (Schlotheim) was due to sexual dimorphism, the microrostrum being *D. irregularis* (Schlotheim). It is probable that this is the case (other examples include *Pleurobelus*; *P. lagenaeformis* (macrorostrum), *P. compressus* (microrostrum), and *Youngibelus*). The epirostrum may fulfil a need to balance some specialized sexual adaptation in the male or female. The male may have had a rather elongate or bulky hectocotylized arm, or the female a brood pouch or similar structure. In either case the centre of gravity would have been affected. It could be that the increased size of one of the sexes may be for visual display used in courtship, as in some modern cephalopods. The relatively light construction and rapid growth of the epirostrum would be suitable for these purposes.

The lack of epirostra in other belemnite groups may point to different levels of specialization. d'Orbigny (1842) described two types of dimorphism; simple and complex (without and with epirostra respectively). The simple type includes dimorphs with relatively small differences in size, and examples have been described by d'Orbigny (1842), Waterston (1952), and Delattre (1956). It may reflect less need for counterbalancing than 'complex' dimorphism. The adult size relationship of the sexes is extremely variable down to the genus level in modern cephalopods (Westermann 1969, p. 19), and this 'simple' and 'complex' dimorphism may represent a similar relationship.

TAXONOMIC IMPLICATIONS

Most ammonite workers (e.g. Makowski 1963; Palframan 1966) consider that dimorphic pairs should be included in one single biological species. However, in the present study the dimorphs are considered separately under two specific names, here included in the same genus (see Callomon 1963).

The startlingly different surface morphologies of the two forms in some way justifies this rather artificial method. As suggested, dimorphism in belemnites may well be on differing levels of complexity and it is probable that most examples are less easy to recognize than the one studied. Therefore, until more dimorphic pairs are recognized it is considered more worth while to retain the separate names, relating to morphospecies, rather than confuse this more practical method by inclusion into one closely defined biological species.

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